

Characterization of photosynthetic pathway of plant species growing in the eastern Tibetan plateau using stable carbon isotope composition

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Abstract

The photosynthetic pathway of plant species collected at Menyuan, Henan, and Maduo sites, east of Tibetan Plateau, China, during the growing season were studied using stable carbon isotopes in leaves. The 232 samples leaves analyzed belonged to 161 species, 30 families, and 94 genera. The $\delta^{13}\text{C}$ values (from -24.6 to -29.2 ‰) indicated that all the considered species had a photosynthetic C_3 pathway. The absence of plant species with C_4 photosynthetic pathway might be due to the extremely low air temperature characterizing the Tibetan Plateau. The average $\delta^{13}\text{C}$ value was significantly ($p < 0.05$) different between annuals and perennials at the three considered study sites. Hence the longer-lived species had greater water-use efficiency (WUE) than shorter-lived species, that is, longer-lived species are better adapted to the extreme environmental conditions of the Tibetan Plateau.

Additional key words: adaptation to environment; alpine meadow; species differences; water use efficiency; $\delta^{13}\text{C}$ values.

Introduction

Photosynthetic pathway of plant species and their relationship to climatic conditions has received much attention by scientists (Hattersley 1983, Li 1993a,b, Redmann *et al.* 1995, Yin and Wang 1997, Tang *et al.* 1999a,b, Qu *et al.* 2001, Wang 2002a,b, 2003). Stable carbon isotope technique is a useful method to investigate C_3 and C_4 photosynthetic pathways. The isotope distribution can reveal information about physical, chemical, and metabolic processes involved in carbon transformations. Bender (1971) and Smith and Epstein (1971) showed that plants utilizing the C_4 pathway had $\delta^{13}\text{C}$ value ($^{13}\text{C}/^{12}\text{C}$) in the range from -6 to -19 ‰, while those utilizing the C_3 pathway from -22 to -34 ‰. These variations have been related to differences in heavy carbon isotope (^{13}C) discrimination by the primary carboxylases. Phosphoenolpyruvate carboxylase has high affinity and low discrimi-

nation to ^{13}C and is associated with C_4 photosynthesis. Ribulose-1,5-bisphosphate carboxylase has lower affinity and higher discrimination to ^{13}C ; it is associated with C_3 photosynthesis.

The environmental conditions of the Tibetan Plateau have influenced the distribution of plant species (Du *et al.* 1995, Wang 1997, Du *et al.* 2003, Hirota *et al.* 2004). There are few reports on the $\delta^{13}\text{C}$ values and photosynthetic pathways of plant species on the Tibetan Plateau (Li *et al.* 1999, Wang 2003). The purpose of the present study was to analyze the photosynthetic pathways based on stable carbon isotope compositions of plant species at three different altitudinal sites in the eastern Tibetan Plateau, Qinghai province, China, where alpine meadow ecosystems are de-paupered.

Materials and methods

Study area: This study was conducted in three counties of Qinghai province, in the eastern Tibetan Plateau. The average altitudes of the considered counties were 3 150,

3 560, and 4 210 m for Menyuan, Henan, and Maduo, respectively (Table 1). The considered counties were dominated by alpine meadow, but there are also few

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semi-desert plants and cushion species. The growing period of plant species was from June to August. The climate of the considered counties was dominated by the southeast monsoon and the high-pressure system of Siberia. The continental monsoon type climate had severe and long winters and short cool summers. The considered counties were characterized by a warm season from May

to August, and a long cold season from November to April. At Menyuan, Henan, and Maduo, the annual average air temperatures were -0.1 , -0.6 , and -3.8 °C, mean maximum air temperatures 26.6 , 26.2 , and 22.4 °C, and mean minimum air temperatures -35.1 , -37.2 , and -48.1 °C, respectively (data from the Qinghai Meteorological Office).

Table 1. Stational and climatic characteristics of the studied counties.

Sites	Altitude [m]	Latitude [°N]	Longitude [°E]	Annu. min. temp. [°C]	Annu. max. temp. [°C]	Annu. mean temp. [°C]	Annu. prec. [mm]	Annu. evap. [mm]	Sunlight duration [h]
Menyuan	3 150	37°26'	101°29'	-35.1	26.6	-0.1	512.0	1 106.6	2 460.6
Henan	3 560	34°50'	101°36'	-37.2	26.2	-0.6	554.9	1 235.3	2 459.3
Maduo	4 210	34°55'	98°13'	-48.1	22.4	-3.8	321.6	1 322.5	2 838.3

Collection and stable carbon isotope analysis: 161 plant species of 30 families and 90 genera were examined (Table 2). Leaf samples for isotope analysis were collected during the growing season (July–August 2003). Each sample consisted of 15–20 leaves from ten plants per species. Leaves were oven dried to constant mass at 75 °C, ground finely, and then sub-sampled for isotopic analysis. Carbon isotope ratios ($\delta^{13}\text{C}$) were determined by

Finnigan MAT DELTA^{PLUS}XL isotope ratio mass spectrometer and calculated by equation of Craig (1957):

$$\delta^{13}\text{C} = \left[\frac{(^{13}\text{C}/^{12}\text{C})_s}{(^{13}\text{C}/^{12}\text{C})_{\text{sta}}} - 1 \right] \times 1000$$

where $(^{13}\text{C}/^{12}\text{C})_s$ and $(^{13}\text{C}/^{12}\text{C})_{\text{sta}}$ are the carbon isotopic ratios of sample and PDB standard, respectively. The overall analytical precision was ± 0.2 ‰.

Table 2. Carbon isotope ($\delta^{13}\text{C}$) values and photosynthetic pathways of plant species grown in the eastern Tibetan plateau, Qinghai, China: A = annual, P = perennial, D = dicotyledon, M = monocotyledon, F = forb, S = sedge, G = grass, Sh = shrub.

Family	Species	Basic characteristics	$\delta^{13}\text{C}$ values			Photosynthetic pathways
			Menyuan	Henan	Maduo	
Boraginaceae	<i>Microula pseudotrichocarpa</i>	D,F,A		-28.9		C ₃
	<i>M. sikkimensis</i>	D,F,A	-28.8		-27.6	C ₃
	<i>M. tibetica</i>	D,F,A		-26.6	-25.9	C ₃
	<i>Trigonotis peduncularis</i>	D,F,P	-26.8			C ₃
Caprifoliaceae	<i>Lonicera minuta</i>	Sh,F,P	-26.5		-26.2	C ₃
Caryophyllaceae	<i>Arenaria bryophylla</i>	D,F,P			-26.1	C ₃
	<i>A. kansuensis</i>	D,F,A			-26.5	C ₃
	<i>Stellaria uda</i>	D,F,P		-26.4		C ₃
Chenopodiaceae	<i>Ajania tenuifolia</i>	D,F,P	-27.9	-27.6	-26.4	C ₃
	<i>Anaphalis lacteal</i>	D,F,P	-28.2	-27.6		C ₃
	<i>Atriplex centralasiatica</i>	D,F,A	-28.0	-26.4	-26.6	C ₃
	<i>A. fera</i>	D,F,A	-27.1			C ₃
	<i>Ceratoides compacta</i>	D,F,A			-27.2	C ₃
Compositae	<i>Artemisia hedinii</i>	D,F,P		-28.2	-26.2	C ₃
	<i>A. scoparia</i>	D,F,P		-27.6		C ₃
	<i>A. sieversiana</i>	D,F,A	-26.9		-27.3	C ₃
	<i>Aster flaccidus</i>	D,F,P	-27.5		-27.0	C ₃
	<i>Cirsium setosum</i>	D,F,P		-26.6		C ₃
	<i>Echinops gmelini</i>	D,F,P		-27.3		C ₃
	<i>Heteropappus altaicus</i>	D,F,P		-26.3		C ₃
	<i>H. gouldii</i>	D,F,P		-27.3		C ₃
	<i>Leontopodium nanum</i>	D,F,P	-27.0	-26.8	-27.3	C ₃
	<i>Ligularia purdomii</i>	D,F,P	-26.5		-25.8	C ₃
	<i>L. sagitta</i>	D,F,P	-26.6			C ₃
	<i>L. virgaurea</i>	D,F,P		-26.9		C ₃

Table 2 (continued)

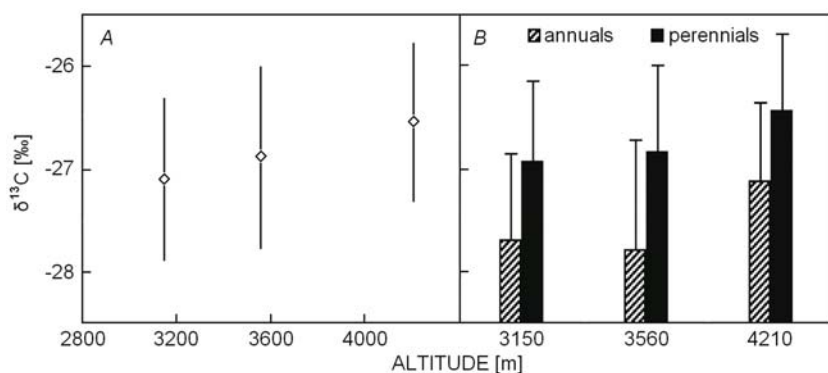
Family	Species	Basic characteristics	$\delta^{13}\text{C}$ values			Photosynthetic pathways
			Menyuan	Henan	Maduo	
Compositae (cont.)	<i>Saussurea amara</i>	D,F,P	-26.6		-26.1	C ₃
	<i>S. arenaria</i>	D,F,P	-27.2	-26.8	-26.7	C ₃
	<i>S. eopygmaea</i>	D,F,P			-27.1	C ₃
	<i>S. katochaete</i>	D,F,P	-26.3			C ₃
	<i>S. kokonorensis</i>	D,F,P	-25.1			C ₃
	<i>S. salsa</i>	D,F,P			-26.5	C ₃
	<i>S. stella</i>	D,F,P			-26.0	C ₃
	<i>S. superba</i>	D,F,P	-27.1	-26.0		C ₃
	<i>Taraxacum mongolicum</i>	D,F,P	-26.0	-27.4	-26.1	C ₃
Cruciferae	<i>Capsella bursa-pastoris</i>	D,F,A	-28.5			C ₃
	<i>Descurainia sophia</i>	D,F,A	-27.1			C ₃
	<i>Draba oreades</i>	D,F,A	-26.9			C ₃
	<i>Hedinia tibetica</i>	D,F,P		-27.2	-25.5	C ₃
	<i>Neotorularia humilis</i>	D,F,P		-27.5	-27.8	C ₃
Cyperaceae	<i>Blysmus sinocompressus</i>	M,S,P	-27.0			C ₃
	<i>Carex atro-fusca</i>	M,S,P		-27.2		C ₃
	<i>C. crebra</i>	M,S,P	-26.5			C ₃
	<i>C. moorcroftii</i>	M,S,P	-27.3		-27.1	C ₃
	<i>C. orbicularis</i>	M,S,P			-25.1	C ₃
	<i>Kobresia capillifolia</i>	M,S,P		-26.4		C ₃
	<i>K. filifolia</i>	M,S,P	-27.3	-27.6		C ₃
	<i>K. humulis</i>	M,S,P	-27.2	-26.5	-26.4	C ₃
	<i>K. pygmaea</i>	M,S,P	-26.2			C ₃
	<i>K. royleana</i>	M,S,P		-26.3	-25.6	C ₃
	<i>K. schoenoides</i>	M,S,P	-26.9			C ₃
	<i>K. tibetica</i>	M,S,P			-27.6	C ₃
<i>Scirpus distigmaticus</i>	M,S,P	-27.3	-27.2	-26.2	C ₃	
Dipsacaceae	<i>Morina chinensis</i>	D,F,P		-24.6		C ₃
Equisetaceae	<i>Equisetum arvense</i>	D,F,P	-25.5			C ₃
Euphorbiaceae	<i>Euphorbia helioscopia</i>	D,F,P		-26.1		C ₃
Gentianaceae	<i>Gentiana aristata</i>	D,F,P	-27.7	-28		C ₃
	<i>G. dahuica</i>	D,F,P	-26.3		-26.7	C ₃
	<i>G. farreri</i>	D,F,P			-26.4	C ₃
	<i>G. leucomelaena</i>	D,F,P	-27.6			C ₃
	<i>G. siphonantha</i>	D,F,P	-26.6	-27.5		C ₃
	<i>G. squarrosa</i>	D,F,P	-26.8			C ₃
	<i>G. straminea</i>	D,F,P	-27.0	-26.2	-25.2	C ₃
	<i>G. tricolor</i>	D,F,A	-27.1			C ₃
	<i>G. zekuensis</i>	D,F,P		-26.3		C ₃
	<i>Gentianopsis paludosa</i>	D,F,A	-27.6		-27.2	C ₃
	<i>Lomatogonium rotatum</i>	D,F,A	-28.5	-27.0		C ₃
	<i>Swertia bifolia</i>	D,F,P	-28.1			C ₃
	<i>S. diluta</i>	D,F,A	-27.7			C ₃
	<i>S. przewalskii</i>	D,F,P	-27.6			C ₃
<i>S. tetraptera</i>	D,F,P	-26.8			C ₃	
Geraniaceae	<i>Geranium sibiricum</i>	D,F,P		-26.6		C ₃
Gramineae	<i>Agrostis perlaxa</i>	M,G,P	-28.0	-27.6		C ₃
	<i>Aneurolepidium dasystachys</i>	M,G,P	-27.7		-27.5	C ₃
	<i>Bromus inermis</i>	M,G,P		-26.9		C ₃
	<i>Elymus nutans</i>	M,G,P	-27.1		-26.8	C ₃
	<i>Festuca ovina</i>	M,G,P	-27.1			C ₃

Table 2 (continued)

Family	Species	Basic characteristics	$\delta^{13}\text{C}$ values			Photosynthetic pathways
			Menyuan	Henan	Maduo	
Gramineae	<i>Festuca rubra</i>	M,G,P	-26.0			C ₃
	<i>Helictotrichon tibeticum</i>	M,G,P	-27.0			C ₃
	<i>Koeleria cristata</i>	M,G,P		-25.5		C ₃
	<i>K. litvinowii</i>	M,G,P	-28.1	-27.9		C ₃
	<i>Poa annua</i>	M,G,A		-27.7	-27.6	C ₃
	<i>P. sinattenuata</i>	M,G,A	-27.1			C ₃
	<i>Ptilagrostis concinna</i>	M,G,P	-25.6			C ₃
	<i>P. dichotoma</i>	M,G,P	-27.2			C ₃
	<i>Stipa penicillata</i>	M,G,P	-25.4			C ₃
	<i>S. purpurea</i>	M,G,P	-26.1		-25.7	C ₃
Iridaceae	<i>Iris ionantha</i>	D,F,P			-26.8	C ₃
	<i>I. potaninii</i>	D,F,P		-26.4		C ₃
Labiatae	<i>Ajuga lupulina</i>	D,F,P	-26.9	-26.6		C ₃
	<i>Dracocephalum heterophyllum</i>	M,F,P		-26.0		C ₃
	<i>Elsholtzia calycocarpa</i>	D,F,A	-25.7			C ₃
	<i>E. densa</i>	M,F,A		-29.0		C ₃
	<i>Lamiophlomis rotata</i>	M,F,P		-27.3		C ₃
	<i>Mentha haplocalyx</i>	D,F,P	-28.8			C ₃
Leguminosae	<i>Astragalus adsurgens</i>	D,F,P			-25.8	C ₃
	<i>A. licentianus</i>	D,F,P	-27.7	-26.4		C ₃
	<i>A. mattam</i>	D,F,P			-26.9	C ₃
	<i>A. peduncularis</i>	D,F,P	-26.6	-26.8		C ₃
	<i>A. polycladus</i>	D,F,P	-26.8	-25.4		C ₃
	<i>Gueldenstaedtia diversifolia</i>	D,F,P			-24.9	C ₃
	<i>G. multiflora</i>	D,F,P	-25.1			C ₃
	<i>Medicago lupulina</i>	D,F,A	-28.7			C ₃
	<i>Oxytropis caerulea</i>	D,F,P	-27.1	-27.3		C ₃
	<i>O. falcata</i>	D,F,P		-28.6	-27.5	C ₃
	<i>O. ochrocephala</i>	D,F,P	-25.7			C ₃
	<i>Thermopsis lanceolata</i>	D,F,P			-26.7	C ₃
	Liliaceae	<i>Allium chrysanthum</i>	M,F,P	-27.3		
Papaveraceae	<i>Hepecoum leptocarpum</i>	D,F,P		-25.3		C ₃
Plantaginaceae	<i>Plantago depressa</i>	D,F,P	-27.8	-27.0		C ₃
Polygonaceae	<i>Polygonum alatum</i>	D,F,A	-27.9	-28.1		C ₃
	<i>P. macrophyllum</i>	D,F,P	-28.0			C ₃
	<i>P. sibiricum</i>	D,F,P	-28.1	-27.7	-26.5	C ₃
	<i>P. tenuifolium</i>	D,F,P	-26.0		-25.8	C ₃
	<i>P. viviparum</i>	D,F,P	-26.5	-26.4	-26.0	C ₃
Potamogetonaceae	<i>Triglochin matitima</i>	M,F,P		-26.8		C ₃
	<i>T. palustre</i>	M,F,P		-25.1		C ₃
Primulaceae	<i>Androsace septentrionalis</i>	D,F,P	-27.1			C ₃
	<i>Glaux maritima</i>	D,F,P	-27.6	-27.7	-26.4	C ₃
Ranunculaceae	<i>Aconitum gymnanandrum</i>	D,F,A	-27.7	-26.7	-26.6	C ₃
	<i>A. pendulum</i>	D,F,P			-27.3	C ₃
	<i>Anemone obtusiloba</i>	D,F,P	-25.3			C ₃
	<i>Delphinium candelabrum</i>	D,F,P	-27.6		-27.3	C ₃
	<i>D. pylzowii</i>	D,F,P	-26.9			C ₃
	<i>Halerpestes tricuspis</i>	D,F,P	-27.6			C ₃
	<i>Oxygraphis glaoiabs</i>	D,F,P		-27.2		C ₃
	<i>Ranunculus brotherusii</i>	D,F,P			-25.0	C ₃

Table 2 (continued)

Family	Species	Basic characteristics	$\delta^{13}\text{C}$ values			Photosynthetic pathways
			Menyuan	Henan	Maduo	
Ranunculaceae	<i>Ranunculus pulchellus</i>	D,F,P	-25.9			C ₃
	<i>R. tanguticus</i>	D,F,P	-27.0	-26.2		C ₃
	<i>Thalictrum alpinum</i>	D,F,P	-26.8			C ₃
	<i>Trollius chinenses</i>	D,F,P		-26.4		C ₃
	<i>T. pumilus</i>	D,F,P	-28.0			C ₃
Rosaceae	<i>Coluria longifolia</i>	D,F,P			-27.2	C ₃
	<i>Dasiphora fruticosa</i>	D,Sh,P	-26.1	-26.0		C ₃
	<i>Potentilla acaulis</i>	D,F,P		-26.5		C ₃
	<i>P. anserina</i>	D,F,P	-28.1		-27.2	C ₃
	<i>P. bifurca</i>	D,F,P		-28.1	-26.9	C ₃
	<i>P. multiceps</i>	D,F,P			-26.0	C ₃
	<i>P. nivea</i>	D,F,P	-27.5			C ₃
	<i>Sibiracea angustata</i>	D,Sh,P	-26.6			C ₃
	<i>Spiraea alpina</i>	D,Sh,P			-25.3	C ₃
Rubiaceae	<i>Galium boreale</i>	D,F,P	-25.8			C ₃
	<i>G. verum</i>	D,F,P	-27.2			C ₃
Salicaceae	<i>Salix oritrepha</i>	D,P	-28			C ₃
Scrophulariaceae	<i>Euphrasia tatarica</i>	D,F,A,	-29.2			C ₃
	<i>Lagotis brachystachya</i>	D,F,P			-27.1	C ₃
	<i>Lancea tibetica</i>	D,F,P	-26.8	-26.0	-26.3	C ₃
	<i>Pedicularis alaschanica</i>	D,F,P	-28.0	-27.2		C ₃
	<i>P. kansuensis</i>	D,F,A	-27.8	-29.1	-27.0	C ₃
	<i>P. longiflora</i>	D,F,A		-28.6	-26.8	C ₃
	<i>P. muscicola</i>	D,F,P		-27.1		C ₃
	<i>P. przewalskii</i>	D,F,P			-27.5	C ₃
	<i>P. roylei</i>	D,F,P		-26.3		C ₃
	<i>Veronica biloba</i>	D,F,A	-27.8	-27.3		C ₃
	<i>V. ciliata</i>	D,F,P				C ₃
Solanaceae	<i>Przewalskia tangutica</i>	D,F,P			-26.0	C ₃
Thymelaceae	<i>Stellera chamaejasme</i>	D,F,P	-26.9		-26.8	C ₃
Umbelliferae	<i>Bupleurum condensatum</i>	D,F,P	-27.7			C ₃
	<i>Notopterygium frobesii</i>	D,F,P	-26.3			C ₃
	<i>N. incisum</i>	D,F,P	-28.1	-26.7		C ₃
	<i>Sphallerocarpus gracilis</i>	D,F,P			-25.8	C ₃

Fig. 1. Average $\delta^{13}\text{C}$ values of (A) plants collected from different altitude, (B) annuals and perennials at different altitudes.

Results

The $\delta^{13}\text{C}$ values of 161 plants collected at three considered sites (Table 1) had a narrow range from -29.2 to -24.6 ‰ (Table 2). The stable carbon isotope ratios for plants in the three sites ranged from -29.2 to -25.1 ‰, -29.1 to -24.6 ‰, -28.8 to -24.9 ‰, respectively, and the average $\delta^{13}\text{C}$ values at each site tended to be more positive with the increase of altitude (Fig. 1A).

There were no significant differences between the average $\delta^{13}\text{C}$ values of monocotyledonous species

(-27.0 ‰) and those of dicotyledonous ones (-26.9 ‰). Thus forbs and shrubs had no different $\delta^{13}\text{C}$ values from monocotyledonous grasses and sedges. Under the same environmental conditions, species with different life span (annuals and perennials) at three sites had significant difference in $\delta^{13}\text{C}$ values ($p < 0.05$). Mean $\delta^{13}\text{C}$ values of annual species tended to be more negative than those of perennial species at each site (Fig. 1B).

Discussion

The $\delta^{13}\text{C}$ values monitored in this study indicate that all the considered plant species belong to C_3 photosynthetic pathway and there are no C_4 species in the eastern Tibetan Plateau. Considering the climate, the low temperature may be the limiting factor for C_4 plant species.

The increase of $\delta^{13}\text{C}$ values of leaves along the considered altitudinal gradient, is in accordance with the results of Körner *et al.* (1988, 1991), Morecroft *et al.* (1990), or Marshall and Zhang (1994). In addition, the $\delta^{13}\text{C}$ values indicate that perennial plants (long-lived plants) have more positive $\delta^{13}\text{C}$ values than annual plants

(short-lived plants), according to Ehleringer and Cooper (1988). The significance of isotopic variation lies in its broad correlation with photosynthetic water-use efficiency (WUE) (Farquhar *et al.* 1982, Hultine and Marshall 2000). Farquhar and Richards (1984) and William *et al.* (1992) showed a positive relationship between WUE and plant longevity based on $\delta^{13}\text{C}$ measurements. Therefore, the results of this study suggest that species with longer lifespan have greater WUE, *i.e.* perennials are more advantageous than annuals in water-limited environments of the Tibetan Plateau.

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